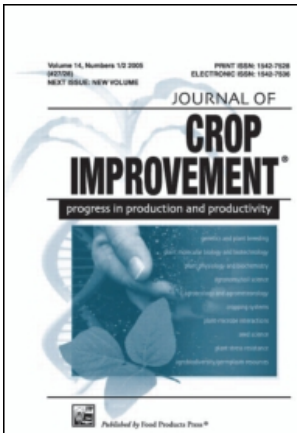

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Mohamed B. Ali[ab]; Amir M. H. Ibrahim[a]; Dirk B. Hays[a]; Zoran Ristic[c]; Jianming Fu[d]
[a] Department of Soil and Crop Sciences, Texas A&M University, College Station, Texas [b] Department of Agronomy, College of Agriculture, Assiut University, Assiut, Egypt [c] USDA/ARS/GMPRC, Kansas State University, Manhattan, Kansas [d] Department of Agronomy, Kansas State University, Manhattan, Kansas

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Wild Tetraploid Wheat (*Triticum turgidum* L.) Response to Heat Stress

MOHAMED B. ALI[1,2], AMIR M. H. IBRAHIM[1], DIRK B. HAYS[1], ZORAN RISTIC[3], and JIANMING FU[4]

[1]*Department of Soil and Crop Sciences, Texas A&M University, College Station, Texas*
[2]*Department of Agronomy, College of Agriculture, Assiut University, Assiut, Egypt*
[3]*USDA/ARS/GMPRC, Kansas State University, Manhattan, Kansas*
[4]*Department of Agronomy, Kansas State University, Manhattan, Kansas*

*Identifying reliable screening tools and characterizing tolerant germplasm sources are essential for developing wheat (*Triticum aestivum *L.) varieties suited for the hot areas of the world. Our objective was to evaluate heat tolerance of promising wild tetraploid wheat (*Triticum turgidum *L.) accessions that could be used as sources of heat tolerance in common- and durum-wheat (*Triticum durum*) breeding programs. We screened 16 wild tetraploid wheat accessions and two common wheat checks for their response to heat stress by measuring damage to the thylakoid membranes, flag leaf temperature depression (FLTD), and spike temperature depression (STD) during exposure to heat stress for 16 days post-anthesis (DPA). Measurements were taken on the day of anthesis then 4, 8, 12, 16 DPA under controlled optimum and heat-stress conditions. Individual kernel weight (IKW) and heat susceptibility index (HSI) measurements were also obtained. Prolonged exposure to heat stress was associated with increased damage to thylakoid membranes, as indicated by the high ratio of constant fluorescence (O) to peak variable fluorescence (P). Some wild tetraploid wheat accessions exhibited a better HSI than the common heat-tolerant wheat cultivar 'Kauz.' A positive and significant correlation was found between O/P ratio and each of FLTD and STD under heat-stress conditions. A negative and significant correlation was found between FLTD and HSI and between STD and HSI based on the second and third measurements (4 and 8*

Address correspondence to Amir M. H. Ibrahim, Department of Soil and Crop Sciences, Texas A&M University, 2474 TAMU, College Station, TX 77843-2474. E-mail: aibrahim@ag.tamu.edu

DPA). Correlations obtained after the third measurement were not significant because of heat-induced, accelerated maturity and a lack of green leaf tissue. This study identified potential heat-tolerant wild tetraploid wheat germplasm that can be incorporated into wheat breeding programs to improve heat tolerance in cultivated common and durum wheat.

*KEYWORDS wild tetraploid wheat, (*Triticum turgidum *L.), heat*

INTRODUCTION

Heat stress is a major abiotic stress factor that limits wheat production worldwide. Different physiological traits associated with heat tolerance have been assayed, including flag leaf temperature depression (FLTD), spike temperature depression (STD), cell membrane thermostability (CMT), triphenyl tetrazolium chloride (TTC) staining, chlorophyll a fluorescence, and reflectance spectroscopy. Canopy temperature depression (CTD), measured with a hand-held infrared thermometer and calculated by subtracting the temperature of the canopy from the ambient air temperature, can be used to evaluate hundreds of lines in a short period of time (Ayeneh et al. 2002; Balota et al. 2007; Bilge et al. 2008). Experiments done under natural field conditions have shown a close association between grain yield of wheat and CTD in hot environments (Reynolds et al. 1994; Fischer et al. 1998). Ayeneh and colleagues (2002) found strong positive correlations between CTD and organ temperature depression, including flag leaves and spikes on one hand and grain yield on the other hand, under heat stress. The presence of awns in the spikes was not associated with heat tolerance (Hatfield et al. 1984).

This contrasts with other findings that postulate a role for awns in continuation of photosynthesis and grain filling following loss of green leaf tissue under heat-stress conditions in wheat and barley (Ferguson, Eslick, & Aase 1973; Johnson et al. 1974; Blum, 1986). In the CMT assay, electrolyte leakage from leaf tissue is measured after exposure to high temperatures (Fokar, Nguyen, & Blum 1998; Ibrahim & Quick, 2001a; Ibrahim & Quick, 2001b). Cellular injury under heat stress can also be assessed spectrophotometerically by quantifying the reduction of TTC to red formazan by mitochondrial dehydrogenase respiratory enzymes in wheat seedlings (Porter et al. 1995; Ibrahim & Quick, 2001a). As explained by Fokar, Nguyen, and Blum (1998), the TTC assay basically evaluates the integrity of the mitochondrial electron-transport chain under heat-stress conditions, and thus it represents respirational activity. Photosynthesis has been reported to be one of the most sensitive processes to heat stress in plants (Demirevska-Kepova et al. 2005), mainly because of the sensitivity of the thylakoid membrane (Takeuchi & Thornber, 1994). Heat damages the nature of photosystem II

(PS II) through removal of the oxygen-evolving enhancer proteins from the thylakoids with no damage to the photosystem I (PS I) complex (Takeuchi & Thornber, 1994). It is believed that damage to the thylakoid membranes caused by heat stress leads to chlorophyll loss that can be easily measured by chlorophyll meters (Ristic, Bukovnik, & Prasad 2007). Chlorophyll fluorescence measurements, on the other hand, require use of fluorometers that require dark adaptation of the leaf tissue, which limits the number of plants that can be screened per day (Ristic, Bukovnik, & Prasad 2007).

Although it cannot be used to process a large number of samples, chlorophyll fluorescence is one of the most powerful techniques available to plant physiologists (Maxwell & Johnson 2000; Sayed, 2003). The ratio of variable fluorescence (Fv), measured as the difference between the maximum and minimum fluorescence, to maximum fluorescence (Fm) is an estimate of PS II maximum efficiency under abiotic stress conditions (Rachmilevitch, DaCosta, & Huang 2006). Premature plant senescence and reduction in the duration of photosynthetic activity also occur under high temperatures (Al-Khatib & Paulsen 1984). Reflectance spectroscopy is another technique that provides a rapid assessment of heat tolerance (Dobrowski et al. 2005; Babar et al. 2006). The spectral reflectance in the visible (VIS) wavelength (400–700 nm) is a function of light absorption by leaf chlorophyll, carotenoids, and anthocyanins (Babar et al. 2006). While most or all of the aforementioned physiological approaches are reliable, closely associated with heat tolerance, and have the potential to be used as screening tools in breeding programs, they have some limitations because of speed of measurement, cost, and labor, e.g., TTC, CMT, spectral reflectance, and chlorophyll a fluorescence. On the other hand, traits such as FLTD, STD, and reflectance spectroscopy require less labor and time and can be used to process thousands of lines by plant breeders and physiologists.

Determining mechanisms associated with heat tolerance and identifying efficient screening assays associated with these mechanisms are vital for improvement of heat tolerance in wheat germplasm (Ristic, Bukovnik, & Prasad 2007). Furthermore, it is crucial to know the association between these essays and grain yield under heat stress to justify their use as selection tools. Pestsova, Börner, and Röder (2006) argued that wheat wild relatives contain valuable genetic sources with high potential for contributing to improvement of heat tolerance in cultivated wheat. In the current study, we evaluated heat tolerance of wild tetraploid wheat by evaluating chlorophyll a fluorescence, FTD, STD, and kernel weight.

MATERIALS AND METHODS

Sixteen wild tetraploid wheat accessions and two common wheat check cultivars (Table 1) were screened for their response to heat stress by measuring

TABLE 1 Sixteen Wild Tetraploid Wheat Accessions and Two Common Wheat Check Cultivars used in the Current Study Along with their Geographical Origin

No.	Species	Cultivar/ Subspecies	Accession no.	Geographical origin
1	*T. aestivum*	Kauz	Check	Mexico
2	*T. aestivum*	Siete Cerros	Check	Mexico
3	*T. turgidum*	*cartlicum*	IG45057	Turkey
4	*T. turgidum*	*cartlicum*	IG45171	Turkey
5	*T. turgidum*	*cartlicum*	IG44999	Turkey
6	*T. turgidum*	*dicoccon*	IG45073	Oman
7	*T. turgidum*	*dicoccon*	IG45303	Ethiopia
8	*T. turgidum*	*dicoccon*	IG45393	Eritrea
9	*T. turgidum*	*dicoccon*	IG45441	Syria
10	*T. turgidum*	*dicoccon*	IG88723	Greece
11	*T. turgidum*	*dicoccon*	IG44961	Turkey
12	*T. turgidum*	*dicoccon*	IG45069	Oman
13	*T. turgidum*	*dicoccon*	IG54388	Georgia
14	*T. turgidum*	*dicoccon*	IG45413	Bulgaria
15	*T. turgidum*	*polonicum*	IG110572	Algeria
16	*T. turgidum*	*polonicum*	IG127682	ICARDA
17	*T. turgidum*	*turgidum*	IG83047	Turkey
18	*T. turgidum*	*turgidum*	IG45448	Ethiopia

damage to the thylakoid membranes, FLTD, STD, individual kernel weight, and HSI. Plant growth conditions and heat treatments were similar to those described by Ristic, Bukovnik, and Prasad. (2007). Briefly, plants of each genotype were grown in 10 pots (Metro Mix 200 potting soil [Hummert Int.], three seedlings per pot) in a greenhouse and were watered daily and fertilized weekly (Miracle Gro fertilizer (24:8:16; Stern's Miracle-Gro Products, Inc., Port Washington, NY)) for the entire duration of the experiment. At the beginning of the flowering stage (50 % of the plants at growth stage Feeks 10.5.1 [Large, 1954]), plants of each genotype were divided into control (five pots) and heat-treatment (five pots) groups. In each group, 10 plants were randomly selected (two plants per pot).

One flag leaf and one spike per selected plant were randomly chosen and tagged (total of 10 flag leaves and 10 spikes per group were tagged). The tagged leaves were later used to measure chlorophyll a fluorescence and FLTD. The tagged spikes were used to measure STD. The treatment group was exposed to heat stress for 16 d (day/night temperature: 36/30°C; relative humidity: 90%–100%; photoperiod: 16/8 h; photosynthetic photon flux [PPF]: 280 μmol m-2 s-1 [Sylvania cool white fluorescent lamps]) in a growth chamber (Conviron, Model PGW-36, Winnipeg, MB, Canada), and the control group was maintained under optimum conditions (day/night temperature: 22/18°C; relative humidity: 90%–100%; photoperiod: 16/8 h; photosynthetic photon flux [PPF]: 280 μmol m-2 s-1 [Sylvania cool white fluorescent lamps]) in a growth chamber (Conviron, Model PGW-36, Winnipeg,

MB, Canada). For each genotype, heat treatment started when 50% of the plants reached Feeks 10.5.1 growth stage (Large 1954).

To avoid or minimize possible dehydration of the leaf tissue during stress treatment, pots of the treatment and control group were kept in trays containing ~1 cm deep water. Chlorophyll a fluorescence, FLTD, and STD were measured after 0, 4, 8, 12, 16 d of heat stress. Chlorophyll a fluorescence was measured in the middle portion of the flag blade (half way between the base and the tip of the blade), as described by Ristic, Bukovnik, and Prasad (2007). Both FLTD and STD were measured in the middle portion of the selected flag leaves and spikes, respectively. The ratio of constant fluorescence (O) and the peak of variable fluorescence (P), i.e., (O/P), was measured to assess the stability of thylakoid membranes (Krause & Weis 1984; Ristic & Cass 1993). Fluorescence measurements were recorded at room temperature (25°C) using a pulse modular fluorometer (Model OS5-FL, Opti-Sciences, Hudson, NH). Data obtained from two plants within one pot were averaged and used for statistical analysis. Both FLTD and STD were measured on two plants in each pot for each treatment using a handheld thermometer (Model AG-42, Teletemperature Crop, Fullerton, CA). Measurements were recorded between 11:00 and 16:00 following Reynolds and colleagues (1998).

At maturity, all plants of each cultivar/treatment (control and heat stress) were harvested and data on yield traits (kernel weight [KW] and number of kernels [NK]) were recorded. Individual kernel weight (IKW) was calculated as follows: IKW = KW/NK. Then IKW was used to calculate HSI, similar to the drought susceptibility index (DSI) calculated by Fischer and Maurer (1978). Using IKW, HSI was calculated, as described by Ayeneh and colleagues (2002). Briefly,

$$HSI = 1 - (Y_b/Y)/1 - (X_b/X),$$

where Y_b is the IKW of each genotype under heat stress and Y is IKW of each genotype under optimum temperature. The variable X_b is the average IKW of all genotypes expressed under heat stress, and X is average IKW of all genotypes under optimum temperatures.

Statistical Analysis

Correlation analysis was used to test the relationship between heat damage to thylakoid membranes and HSI, FLTD, and STD; FLTD and HSI; and STD and HSI. The PROC CORR PEARSON procedure in the Statistical Analysis System (SAS Institute, 2003) was used to quantify the relationship between the variables.

RESULTS AND DISCUSSION

Assessment of heat tolerance in 16 wild tetraploid wheat accessions and two common wheat check cultivars, namely 'Kauz' and 'Siete Cerros,' was carried out by evaluating damage to thylakoid membranes using chlorophyll a fluorescence. Heat-stress-caused damage to thylakoid membranes (Ristic, Bukovnik, & Prasad 2007) could be measured by O/P ratios using a fluorometer. Genotypes responded differently to heat stress. The most heat-susceptible genotypes, as indicated by the high O/P ratios, were the wild tetraploid wheat accessions IG45413, IG88723, IG127682, and IG110572 (O/P > 439% after 16 d of heat stress; Figure 1). We found O/P < 186% after 16 d of heat stress in the check cultivar Siete Cerros, and wild wheat accessions IG45069, IG45393, and IG45057. Heat tolerance associated with lesser damage to photosystem II has been attributed to elongation factors EF-Tu (Bhadula et al. 2001; Ristic et al. 2006).

In many breeding programs, where heat stress is a major abiotic stress factor, grain yield and its components are used as the main selection criteria (Ehdaie, Waines, & Hall 1988). The HSI has been used to determine relative stress injury, as it accounted for variation in both yield potential and performance under stress conditions (Bruckner & Frohberg 1987). Lower stress susceptibility (S < 1) is synonymous with higher stress resistance (Fischer & Maurer, 1978). In this study, the HSI ranged from 0.353 in IG45069 to 1.756 in IG45413 (Table 2). The HSI for the checks Siete Cerros and Kauz were 0.651 and 1.162, respectively. These results show that some of the wild tetraploid accessions were better than the heat-tolerant checks, emphasizing the potential of including these accessions in crossing blocks of breeding programs dedicated to improving heat tolerance of common and durum wheats.

We analyzed the relationship between HSI and O/P ratio of chlorophyll a fluorescence under heat stress as percent of control at 0, 4, 8, 12, and 16 d of heat stress. A positive and significant correlation was found when data were plotted and analyzed for each single day of heat stress, except for day 0 (Figure 2 and Table 3). The correlation coefficients ranged from 0.33 ($P = 0.187$) for day 0 to 0.93 ($P < 0.0001$) for day 16. It is apparent from these results that the correlation coefficients and their degree of significance increased as the duration of exposure to heat stress was prolonged. The high positive correlation between HSI and O/P ratio of chlorophyll a fluorescence under heat stress in this study can be attributed to the following: 1) increasing exposure to heat stress led to more damage to thylakoid membranes, as indicated by the high O/P ratios; and 2) heat stress decreased both the rate and duration of photosynthesis, which may have led to decreased kernel filling.

We investigated the relationship between FLTD and STD at 0, 4, 8, 12, and 16 d of heat stress (Figure 3). Positive and significant correlations were found except at 0 d of heat stress (Table 4). The correlation ranged from 0.45 ($P = 0.06$) to 0.99 ($P = 0.000$) for day 0 and 8, respectively.

The high positive and significant correlations between FLTD and STD under heat stress indicate that we can use either FLTD or STD to assess heat stress tolerance.

The correlation between FLTD and STD, on one hand, and HSI, on the other hand, was negative and significant for 4 d and 8 d of heat stress. On

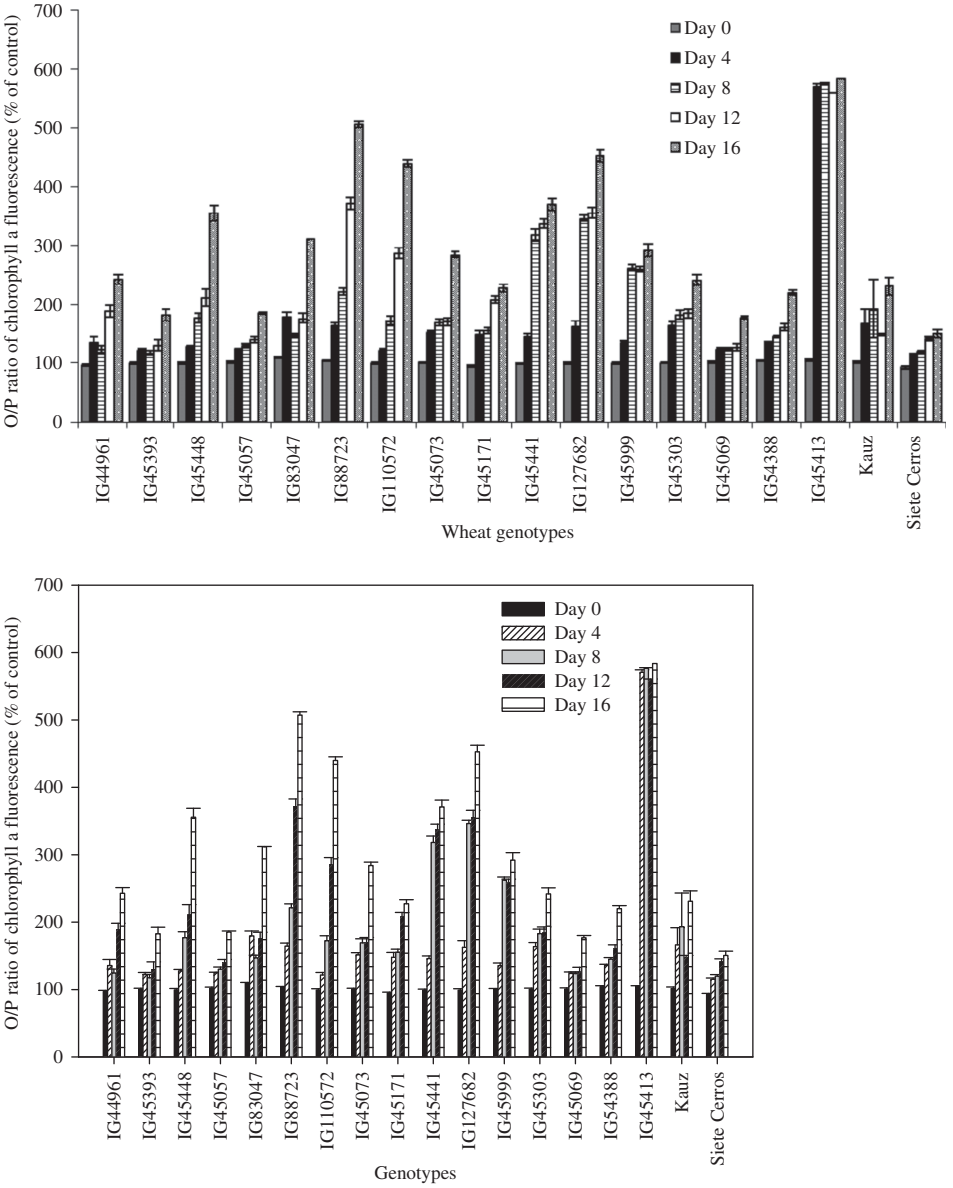


FIGURE 1 The ratio of constant fluorescence and the peak of variable fluorescence (O/P) of 16 wild tetraploid wheats and two hexaploid spring wheats under heat stress conditions. (Chlorophyll a fluorescence was measured on the same flag leaves after 0, 4, 8, 12, and 16 d of exposure to heat stress. Bars indicate means ± standard errors; n = 10.)

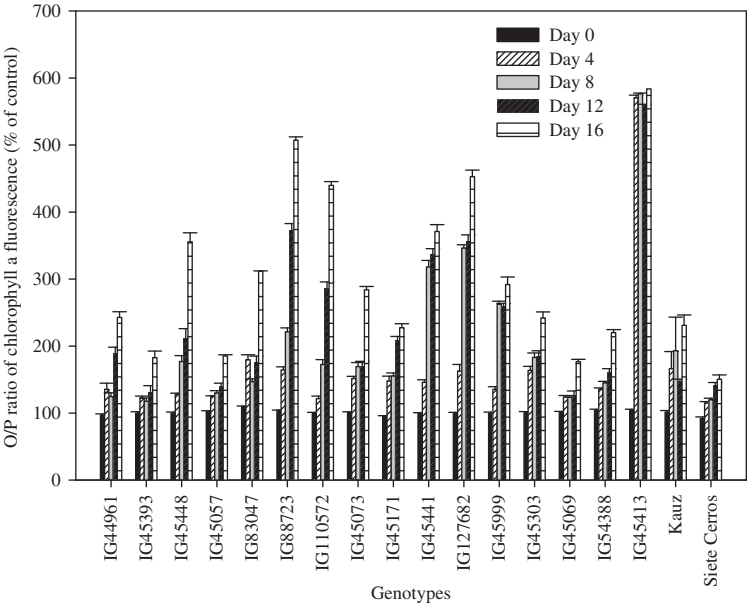


FIGURE 1 (Continued).

TABLE 2 Individual Kernel Weight (IKW), under Both Optimum and Heat Stress (HS) Conditions, and Heat Susceptibility Index (HSI) of 16 Wild Tetraploid Wheat Accessions and Two Common Wheat Check Cultivars

Genotypes	IKW – optimum	IKW – HS	HSI
IG83047	0.0551	0.0243	1.049
IG45073	0.0381	0.0193	0.927
IG45303	0.0297	0.0170	0.800
IG45393	0.0401	0.0300	0.472
IG45441	0.0352	0.0138	1.141
IG88723	0.0369	0.0069	1.528
IG110572	0.0478	0.0156	1.263
IG45057	0.0374	0.0233	0.706
IG45171	0.0297	0.0192	0.663
IG44961	0.0298	0.0155	0.903
IG127682	0.0532	0.0125	1.436
IG45448	0.0385	0.0151	1.139
IG45999	0.0316	0.0152	0.976
IG45069	0.0311	0.0252	0.353
IG45388	0.0337	0.0223	0.637
IG45413	0.0329	0.0021	1.756
Kauz	0.0322	0.0123	1.162
Siete Cerros	0.0330	0.0216	0.651

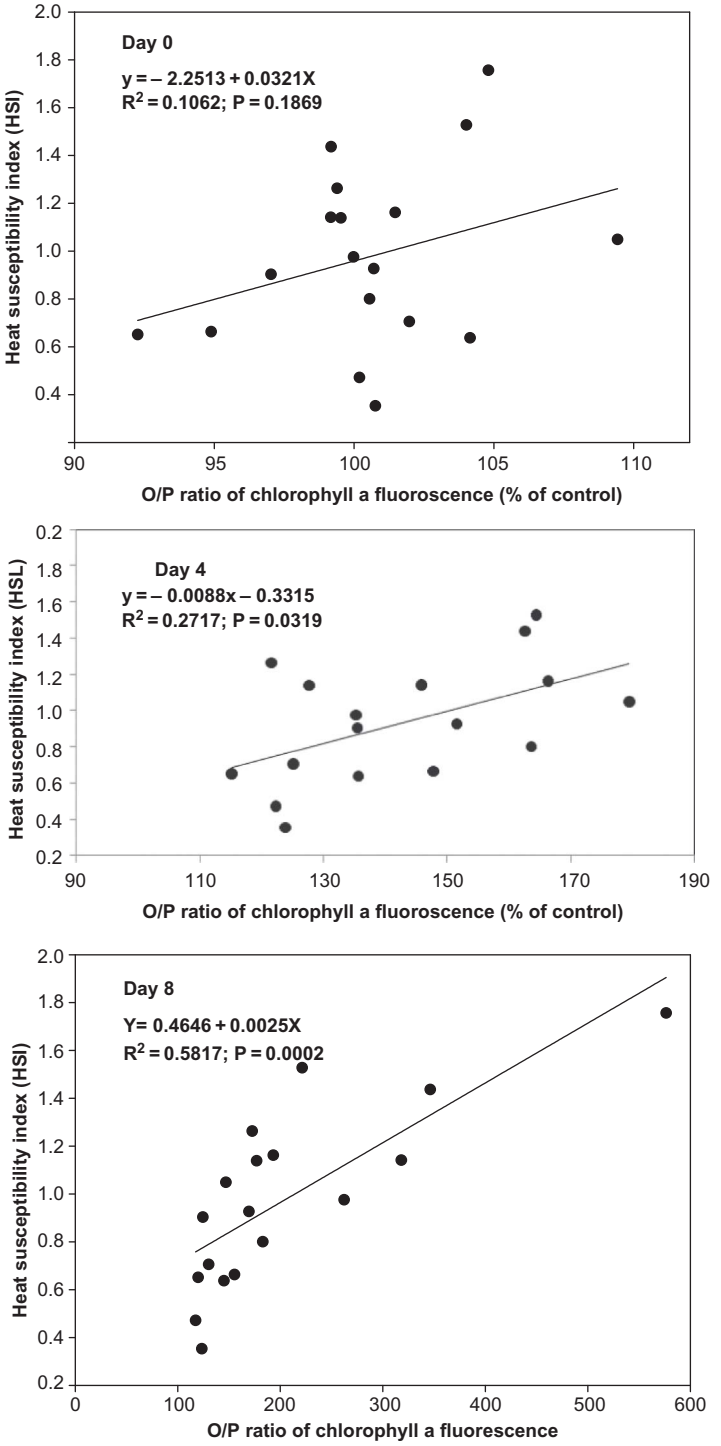
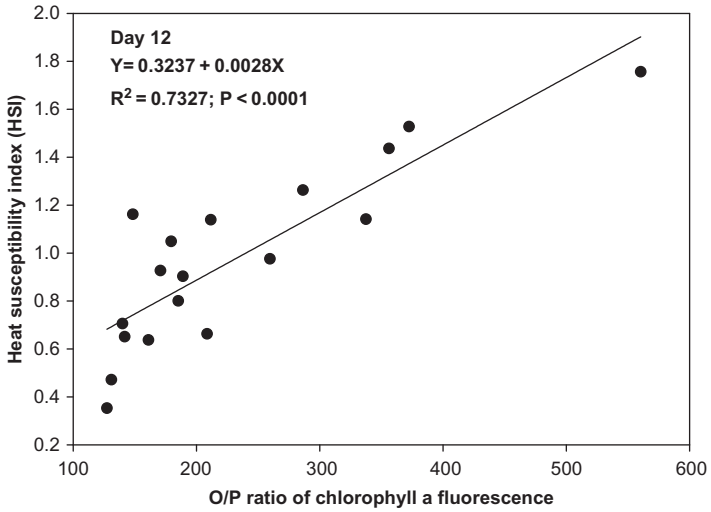


FIGURE 2 The association between O/P ratio of chlorophyll a fluorescence (% of control) and heat susceptibility index (HSI) at day 0, 4, 8, 12, and 16 of post-anthesis heat treatment.



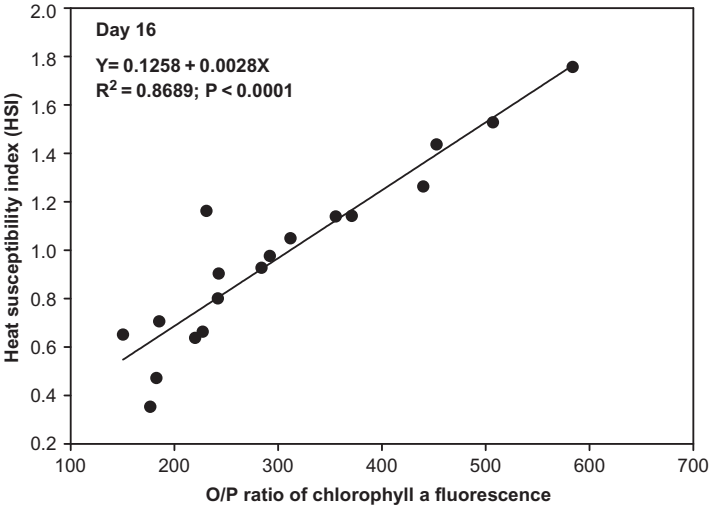


FIGURE 2 (Continued).

TABLE 3 Correlation Coefficients Between O/P Ratio of Chlorophyll a Fluorescence (% of Control) and HSI at day 0, 4, 8, 12, and 16 of Post-Anthesis Heat Treatment

Days of heat stress	DF	R-value	P-value
Day 0	16	0.326	0.1871
Day 4	16	0.521	0.0319
Day 8	16	0.762	0.0002
Day 12	16	0.856	< 0.0001
Day 16	16	0.932	< 0.0001

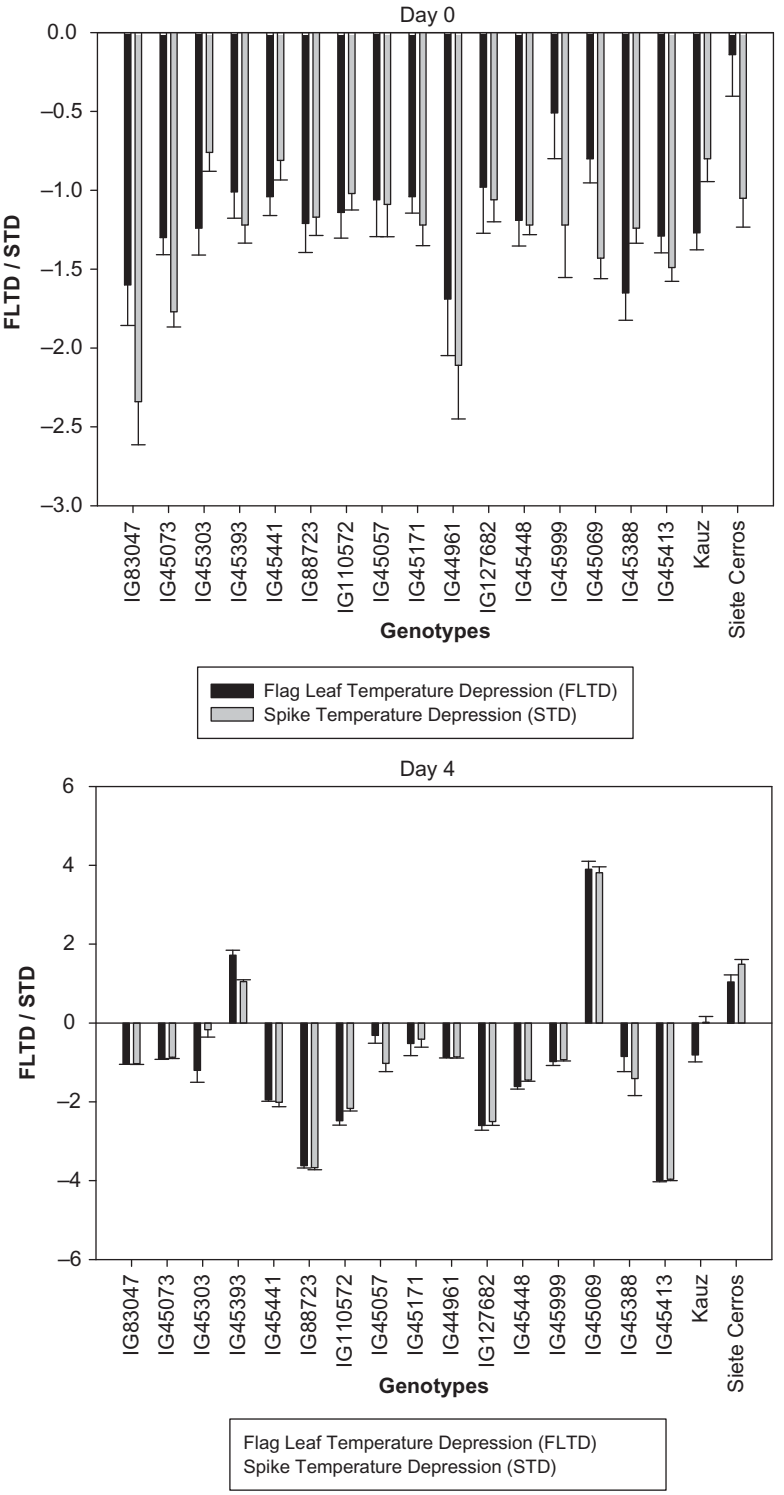


FIGURE 3 The relationship between flag leaf temperature depression (FLTD) and spike temperature depression (STD) at 0, 4, 8, 12, 16 d of heat stress.

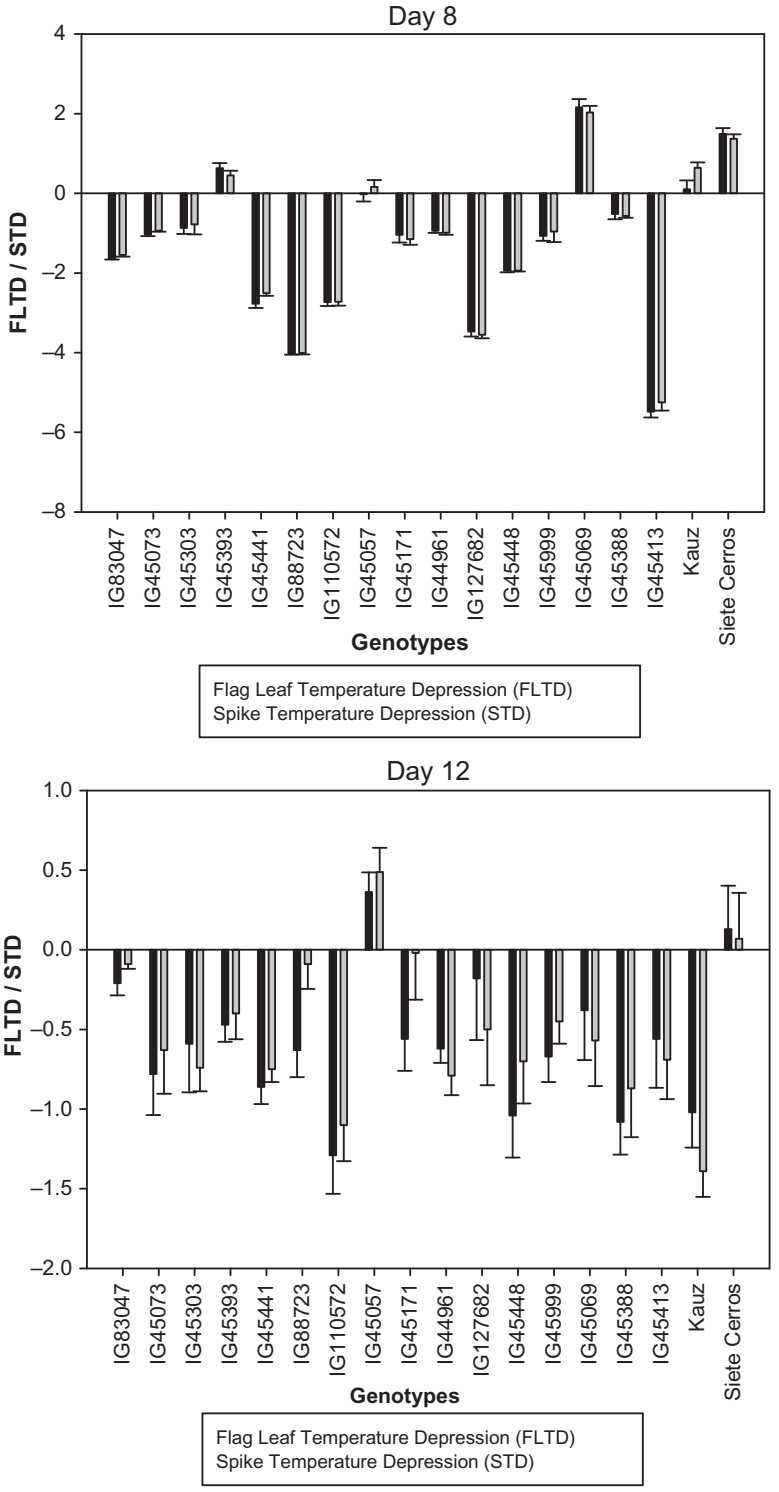


FIGURE 3 (Continued).

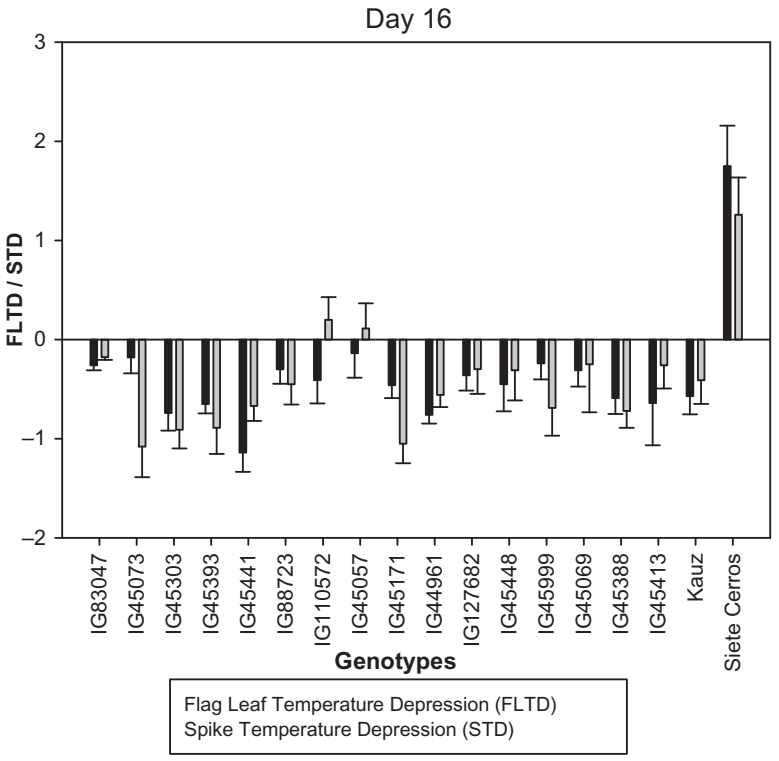


FIGURE 3 (Continued).

TABLE 4 Correlation Coefficients Between Flag Leaf Temperature Depression (FLTD) and Spike Temperature Depression (STD) at Day 0, 4, 8, 12, and 16 of Post-Anthesis Heat Treatment

Days of heat stress	DF	R-value	P-value
Day 0	16	0.452	0.060
Day 4	16	0.971	0.000
Day 8	16	0.996	0.000
Day 12	16	0.823	< 0.00003
Day 16	16	0.763	0.0002

the other hand, the correlations at 0, 12, and 16 d were not significant. The lack of correlation at 12 and 16 d of heat stress could be attributed to the lack of green-leaf tissue from 12th post-flowering onwards under the heat-stress conditions. In general, the correlation between STD and HSI was lower than that between FLTD and HSI (Table 5).

The positive association for grain-filling rate vs. FLTD and STD in other studies indicated that cooler genotypes had longer grain-filling rates (Ayeneh et al. 2002). Negative associations of STD and CTD with HSI were found (Ayeneh et al. 2002); however, a positive correlation was reported between

TABLE 5 Correlation Coefficients Between Flag Leaf Temperature Depression (FLTD), Spike Temperature Depression (STD) and Heat Susceptibility Index (HSI) at Day 0, 4, 8, 12, and 16 of Post-Anthesis Heat Treatment

		FLTD		STD	
Days of heat stress	DF	R-value	P-value	R-value	P-value
Day 0	16	−0.2284	0.36205	0.02578	0.9191
Day 4	16	−0.9034	0.0000003	−0.8562	0.0000058
Day 8	16	−0.9134	0.0000001	−0.8888	0.0000008
Day 12	16	−0.2591	0.29921	−0.25013	0.31679
Day 16	16	−0.2190	0.382588	0.05897	0.816185

HSI and CTD. Therefore, canopy temperature can be used as a tool in the selection of wheat targeted to dry production areas (Blum et al. 1989). Similarly, we can use FLTD and STD as tools for selecting wheat targeted to heat-stressed environments. The strong correlations between either FLTD or STD and HSI at 4 and 8 d of heat stress indicate that both FLTD and STD, measured by infrared thermometers, are reliable and efficient means of assessing heat stress tolerance in wheat.

In conclusion, our study revealed a high significant positive correlation between damage to thylakoid membranes and HSI under heat stress. The results suggest that chlorophyll a fluorescence measured by a pulse modular fluorometer is a reliable tool for screening for heat tolerance in wheat. Our study also showed that FLTD and STD were positively and significantly associated with one another, on one hand, and with HSI, on the other hand. These results suggest that either FLTD or STD can be used as a reliable tool for screening for heat tolerance in wheat. This study also showed that wild tetraploid wheat had excellent heat tolerance, suggesting that it can be included in crossing blocks of breeding programs aimed at improving heat tolerance in common and durum wheats.

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